

OPINION

Can common mycorrhizal fungal networks be managed to enhance ecosystem functionality?

Pierre-Louis Alaux¹  | Yaqian Zhang¹  | Lucy Gilbert²  | David Johnson¹ 

¹Department of Earth and Environmental Sciences, The University of Manchester, Manchester, UK

²Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

Correspondence

Pierre-Louis Alaux, Department of Earth and Environmental Sciences, Michael Smith Building, The University of Manchester, Oxford Road, Manchester M139PT, UK.
Email: pierre-louis.alaux@manchester.ac.uk

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Societal Impact Statement

Mycorrhizal fungi are key components of soil biodiversity that offer potential to provide sustainable solutions for land management, notably in agriculture and forestry. Several studies conducted in controlled environments show that key functional attributes of common mycorrhizal networks (CMNs), which inter-link different plants, are influenced by management practices. Here, we highlight the need to consider how land management affects the ubiquity and function of CMNs in nature to maximize the role of mycorrhizal fungi in enhancing ecosystem services. We emphasize that CMNs can sometimes negatively affect aspects of plant performance, but there remain major gaps in understanding before explicit consideration of CMN management can be delivered.

Summary

Most mycorrhizal fungi have the capacity to develop extensive extraradical mycelium, and thus have the potential to connect multiple plants and form a 'common mycorrhizal network'. Several studies have shown that these networks can influence plant establishment, nutrition, productivity and defense, nutrient distribution and storage, and multitrophic interactions. However, many of these studies have focused on the importance of common mycorrhizal networks in ecological contexts and there has been less emphasis in managed systems, including croplands, grassland, agroforestry and forestry, on which humankind relies. Here we review the evidence of the potential importance of common mycorrhizal networks in managed systems, and provide insight into how these networks could be managed effectively to maximize the functions and outputs from managed systems. We also emphasize possible negative effects of common mycorrhizal networks on plant performance and question popular views that mycorrhizal networks may offer a panacea for enhancing ecosystem services. We highlight the need to gain greater insight into the ubiquity, functioning, and response to management interventions of common mycorrhizal networks and, critically, the need to determine the extent to which these networks can add value to the promotion of mycorrhizal colonization.

KEYWORDS

agroecosystems, forestry, land management, plant to plant signaling, restoration, soil biodiversity, sustainable agriculture

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1 | INTRODUCTION

Mycorrhizal fungi are largely obligate biotrophs forming associations with the majority of terrestrial plant species (Brundrett & Tedersoo, 2018), and often form complex and (usually) dense networks of extraradical mycelium (ERM) in soil (Miller et al., 1995). The ERM forages soil that is not accessible to the root system thus granting increased access to elements that are needed in large amounts by host plants, notably phosphorus (P) and nitrogen (N; Wipf et al., 2019). A fascinating feature of the ERM is its capacity to interconnect numerous plants belonging to the same or different species (Rhodes, 2017; Simard, 2018; Simard et al., 1997), forming common mycorrhizal networks (CMNs), often coined the ‘wood-wide web’(Rhodes, 2017).

The potential functional consequences of such underground physical connections linking individual plants challenge our thinking of resource capture and multitrophic interactions, and as a result has spawned numerous popular views, sometimes exaggerated, extolling the virtues of CMNs for both natural and managed systems (Simard, 2018). Such enthusiasm for CMNs is not surprising given their functional capabilities. Indeed, CMNs formed by arbuscular mycorrhizal (AM) fungi have been shown to facilitate movement of water (H₂O; Egerton-Warburton et al., 2007), and significant amounts of P (Mikkelsen et al., 2008) as demonstrated through the use of radioisotopes. CMNs formed by ectomycorrhizal (ECM) fungi have been shown to facilitate transfer of carbon (C; Selosse et al., 2006; Rog et al., 2020), N (He et al., 2005) and

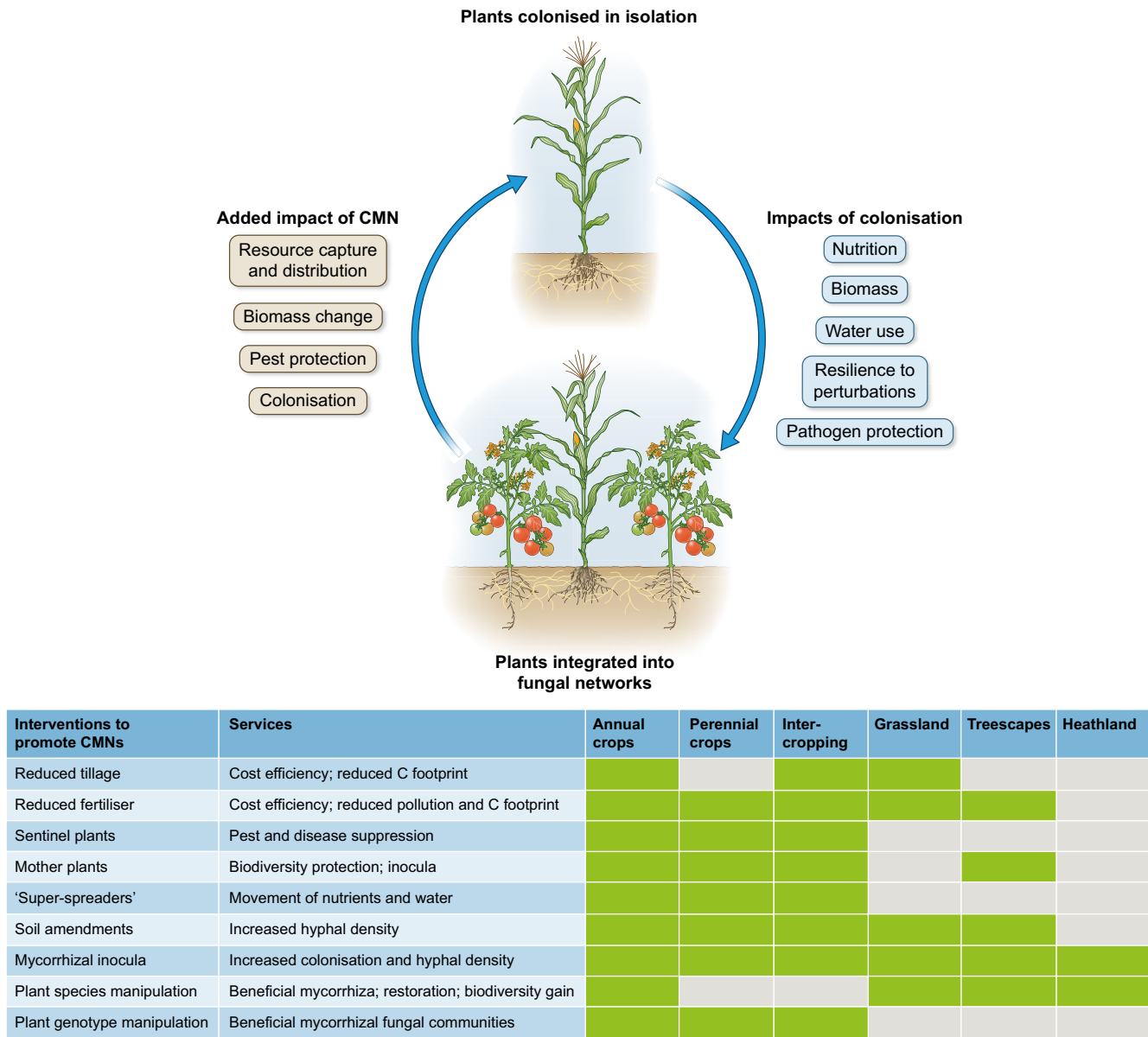


FIGURE 1 Impacts of mycorrhizal colonization and integration of plants into common mycorrhizal networks. The arrows indicate a hypothetical virtuous circle in which promotion of colonization may lead to more abundance CMNs, which leads to more effective colonization of seedlings. Green shading highlights those interventions and services that have greatest potential to be implemented in specific ecosystems

H₂O (Simard et al., 2015). Furthermore, involvement of CMNs is not limited to nutrient exchange but can also involve allelochemicals (Barto et al., 2011) for AM fungi, and defence information (Gilbert & Johnson, 2017; Oelmüller, 2019) for both ECM and AM fungi, which can impact multitrophic interactions (Gilbert & Johnson, 2015).

Therefore, CMNs can actively participate in the well-documented beneficial effect of mycorrhizal fungi on plant nutrition (Smith & Read, 2008) as well as improving plant resistance and tolerance to abiotic (e.g. drought; Plouznikoff et al., 2016) and biotic (Whipps, 2004) stresses. Thus, there is growing evidence of the multifunctional effects of CMNs across ecosystems involving different types of mycorrhizal fungi. A burgeoning literature and plethora of commercial products and organizations have focused on promoting mycorrhizal fungal colonization of plants of interest (i.e. horticultural or crop species), especially those forming arbuscular mycorrhizas (Berruti et al., 2016; Chen et al., 2018). Yet, there remain few attempts to explicitly manage CMNs to enhance valuable ecosystem services, and tackle globally important grand challenges related to sustainable agriculture, production of fuel and fiber, water use and biodiversity conservation. Therefore, new information to inform guidance on how best to manage ecosystems is required.

This need is particularly important because many of Earth's terrestrial ecosystems have been managed to some extent; a recent consensus view estimates that 51% of land area has been modified for human purposes (Hooke et al., 2012). This estimate includes the areas used for croplands (13%) and pasture grassland (23%), and planted (2.1%) and logged (1.8%) forest, as well as urbanization. Additionally, humans may influence unmanaged 'natural' systems indirectly due to anthropogenic activities (e.g. foraging, hunting, pollutant deposition). Thus, a vast range of specific land-uses are potentially affected by how humans influence mycorrhizal fungi (Rillig et al., 2019) and the CMNs that they develop. Nevertheless, agroecosystems, including crops and grassland, and forests, productive forestry, agroforestry and forest restoration and creation, are the primary systems of interest from the perspective of CMNs.

Here, we provide an overview of the evidence of the potential importance of CMNs in managed systems and provide insight into how CMNs could be managed effectively to maximize the functions and outputs from these systems with reduced farming C cost. Indeed, conventional farming often has a high C cost notably by over fertilization or pest management and tillage (C footprint, Figure 1; Hillier et al., 2009). Crucially, we also emphasize the need to consider potential negative effects of CMNs on plant performance, and to ensure popular views of CMN function are evidence-based, so that effective management strategies can be carefully developed. CMNs are intrinsically linked to the need for plants both to form mycorrhizas and produce ERM (Rhodes, 2017). Therefore, this synthesis inevitably considers hyphal production and density alongside our focus on the added impact (see Figure 1) gained through explicit consideration of CMNs in managed ecosystems.

2 | HOW WIDESPREAD IS THE 'WOOD-WIDE WEB'?

In order to effectively manage CMNs, we need to have reliable data both on their ubiquity and extent, but also their functionality over distance. Alas, such information remains scarce, especially in AM dominated systems, despite previous calls to collect such data (Babikova et al., 2014), no doubt because of the difficulty in reliably estimating the presence and extent of CMNs. Notable exceptions include information on the extent of CMNs formed by particular species of ECM fungi in temperate forests in the US (Simard & Durall, 2004) and Canada (Beiler et al., 2010). For example, CMNs formed by *Rhizopogon* spp. Fr. extended across a 20 m × 20 m plot and often interconnected several trees (Beiler et al., 2010). Nevertheless, we need far more studies of this kind before broad statements about CMN ubiquity in forests and woodland can be relied upon. Heathland vegetation dominated by ericaceous species also supports extensive ERM, but the fine roots of the host plants which are adept at foraging through soil mean that the fungi are generally confined close to their surface. Some of the fungi forming ericoid mycorrhizas can also form CMNs but these generally occur at localized scales (Kjøller et al., 2010). Remarkably, some fungi can simultaneously form classic ectomycorrhizas on trees and ericoid mycorrhizas on ericaceous shrubs, although these CMNs are also restricted to distances <4 cm (Grelet et al., 2010; Kjøller et al., 2010).

It is often assumed (especially in the popular science press) that CMNs formed by both AM and ECM fungi can cover large areas, potentially at field scales. Such enormous networks are unlikely to form in nature, but more information is needed to objectively interpret the extent of CMNs formed by mycorrhizal fungi in different contexts, particularly managed systems dominated by AM-forming plants. The classic work of Chiariello et al. (1982) measured transfer of ³²P up to 9 cm in intact grassland turfs, although an unequivocal role of a CMN in this transfer was not possible. In the laboratory, Mikkelsen et al. (2008) demonstrated transfer of ³²P by a CMN over 20 cm, indicating the potential for CMNs to influence nutrient dynamics at relatively large scales by several individual plants, depending on grassland type.

Increasing numbers of studies have quantified hyphal density (Kim et al., 2013) and even hyphal turnover (Hagenbo et al., 2017) by both ECM and AM fungi, including in managed ecosystems (Table 1). The often large densities of hyphae in soil in itself provides strong evidence for the potential to form CMNs, and perhaps this information is adequate to infer the presence of CMNs from a management perspective, without the need to undertake expensive, technically challenging, and time-consuming molecular or functional analyses. Nevertheless, we argue that greater focus is needed to quantify how land-management practices affect the ability of mycorrhizal fungi to form functional and stable networks, and provide more rigorous test of the hypothesis that ERM density is an adequate proxy for CMN formation. Moreover, relatively simple experiments could also be undertaken to confirm the ability of different mycorrhizal fungi to form CMNs under controlled

TABLE 1 Typical hyphal densities in soil from ecosystems with contrasting land use and management

Managed ecosystem	Location	Soil type	Plant species	Hyphal density (m/g)	Reference
Grassland	Batavia, USA	Mundelein silt loam	Tallgrass prairie	76–111	Miller et al. (1995)
Grassland	Batavia, USA	Mundelein silt loam	Ungrazed pasture	52–81	Miller et al. (1995)
Grassland	Nunn, USA	Sandy loam	Shortgrass prairie	29–117	Ingham et al. (1986)
Grassland	N Missoula, USA	Sandy loam	Idaho fescue, Bluebunch wheatgrass	50	Lutgen et al. (2003)
Annual crop	Elora, Canada	Pasteurized soil	Maize (<i>Zea mays</i> L.)	16.3–60	McGonigle and Miller (1999)
Annual crop	Hessen, Switzerland	Mixture of sterile soil and sand	Maize	7.0–19.0	Frey and Schüepp (1993)
Annual crop in no-till	Quebec, Canada	Sandy loam	Maize	10.7–137.3	Kabir et al. (1997)
Annual crop in conventional tillage	Quebec, Canada	Sandy loam	Maize	14.5–130.1	Kabir et al. (1997)
Saline ecosystem	Chifeng, China	Loam	Black locust (<i>Robinia pseudoacacia</i> L.)	10.9	Sheng et al. (2019)
Saline ecosystem	Dengkou, China	Sandy loam	Black locust	11.7	Sheng et al. (2019)
Saline ecosystem	Pingluo, China	Clay	Black locust	6.1	Sheng et al. (2019)
Saline ecosystem	Dunhuang, China	Loam	Black locust	14.7	Sheng et al. (2019)
Tropical forest	Cordillera Real, USA	Stagnic Cambisol	Evergreen lower montane forest	10.4	Camenzind and Rillig (2013)
Plantation forest	Otsu City, Japan	Cambisol on granite bed Rock	Evergreen broad-leaf shrubs, mainly <i>Eurya japonica</i> Thunb.	1.08	Schäfer et al. (2019)
Tropical forest	Borneo, Malaysia	Ultisol	Selectively logged tropical forest	2.7	Robinson et al. (2020)
Oil palm plantation	Borneo, Malaysia	Ultisol	<i>Elaeis guineensis</i> Jacq.	0.6	Robinson et al. (2020)
Orchards (sod culture)	Wuhan, China	Yellow sandy clay	Satsuma mandarin trees, Bahia grass	1.15	Wang et al. (2012)
Orchards (herbicide treated and no-tillage)	Wuhan, China	Yellow sandy clay	Satsuma mandarin trees	0.94	Wang et al. (2012)
Hillside citrus orchards	Zigui, China	Calcareous purple soil	Citrus trees, red tangerine	1.39–2.57	Wang et al. (2013)
Pots in the lab	Tåstrup, Denmark	Mixture of sandy moraine loam and quartz sand	Subterranean clover	25	Mikkelsen et al. (2008)
Compartment in the lab	Beijing, China	Calcareous Luvisol	Wheat (<i>Triticum aestivum</i> L.)	0.19–0.62	Yao et al. (2001)
Restored coal mine	Lincoln, USA	Clay loam	Native grassland including <i>Agropyron smithii</i> Rydb. and <i>A. dasystachyum</i> Hook. Scribn.	54	Allen and Allen (1986)

conditions. The assumption is that all mycorrhizal fungi have this capacity, but a systematic test has not been done. The capacity to form CMNs may indeed be a functionally important trait that adds to the growing number of studies using traits to shed new light on the functional significance of microbial diversity (de Bello et al., 2010; Fry et al., 2019; Wang et al., 2019).

In soil, the ERM can represent between 20% and 30% of the total soil microbial biomass (Leake et al., 2004) and frequently accounts for tens, and sometimes up to a hundred m of hyphae per cm³ of soil (Miller et al., 1995). Growth rates of mycorrhizal fungi (calculated by dividing total hyphal length by the number of days growth) can be fast: in vivo model systems

using AM fungi estimated growth rates of 738–1,067 mm day⁻¹ (Giovannetti et al., 2001), thus indicating great potential of fungi to interconnect many individual roots. Anastomosis between ERM of different AM host plants has been observed (Novais et al., 2017) and the frequency of fusions between hyphae coming in contact was high (67%–77%), as was the number of fusions along hyphae (0.46–0.51 mm⁻¹; Novais et al., 2017). The speed of CMN formation varies depending on the environmental conditions, notably the growing medium and distance between plants. Indeed, the latter stages of colonization of the potato variety Bintje has been obtained after 12 days using in vitro CMN (Gallou et al., 2010), whereas it was observed after

35 days after inoculation for tomato in a pot experiment (Song et al., 2010).

Direct exploration of the network topology (i.e. the arrangement of the various elements of a communication network such as nodes and links; Simard, 2018) of belowground fungi are difficult to explore in nature. Nevertheless, such analyses are beginning to alter the conventional view by showing that both AM and ECM fungal clades include host-specific and generalist fungi (Toju et al., 2015). Generalist fungi have broad host ranges potentially working as interaction network hubs in plant-fungus networks and thereby connecting otherwise isolated groups of plants (Olesen et al., 2007). In forests, plants and fungi were associated with a narrower range of partners than expected under models that assumed random associations between hosts and symbionts, and the networks were compartmentalized into modules of closely associated plants and fungi (Toju et al., 2015). In those networks some trees were linked with up to 48 other trees, forming distinct hubs (Simard, 2018). The ability of some ECM fungi to form such inter-connected networks clearly offers opportunities for exploitation to enhance key ecosystem services related to forestry and forest restoration.

3 | FUNCTIONAL ATTRIBUTES OF CMNS RELEVANT TO MANAGEMENT INTERVENTIONS

Here, we outline some of the key functional attributes of CMNs that offer the most potential to be influenced by management practices or, conversely, which may detrimentally affect plant performance (Figure 1). Most studies in this area have been conducted under simplified and controlled experimental settings and there is much work to be done to test the significance of these findings under more realistic field-based conditions. Nevertheless, we illustrate potential guidance for land managers (Figure 1); notably, we highlight that farming systems with light to no-till, cover crops and use of simultaneously diverse crops are expected to make the best use of CMNs.

3.1 | Colonization of seedling recruits

The ability of plant seedlings to become established is critical for their survival and becoming rapidly colonized by beneficial mycorrhizal fungi facilitates this process. From a management perspective (e.g. when creating new woodland, promoting establishment of species of conservation concern, growing food crops) ensuring that focal plants become rapidly colonized by beneficial fungi is therefore important.

Laboratory experiments consistently show that CMNs promote fast and homogenous colonization of seedling recruits (Gallou et al., 2010; Marquez et al., 2018; Voets et al., 2009).

Demonstrating such effects in the field is more challenging, and experiments often rely on mesh cores (e.g. Johnson et al., 2001) to manipulate seedling access to ERM supported by surrounding adult

plants. This approach is not perfect because, first, it is rarely possible to unequivocally determine whether a seedling is connected to a wider CMN and, second, the mechanism of how a seedling benefits (or not) from integration into a CMN is difficult to quantify (e.g. resource transfer from a neighbouring adult plant; transfer of resources by mycorrhizal fungi from volumes of soil otherwise unavailable to the seedling; increased pathogen protection). Despite these limitations, mesh cores remain a key method for field manipulation of CMN presence, and their use has shown how CMNs promote the establishment of new recruits in grassland (Van der Heijden & Horton, 2009) and forests (e.g. Booth, 2004; Liang et al., 2020; Nara, 2006). Booth and Hoeksema (2010) used a trenching approach to show that connection to CMNs formed by ECM had positive effects on seedling establishment and benefited notably from increased access to soil water. Furthermore, in stressful environments (e.g. in saline soils) adult plants can promote the growth and nutrient uptake of their seedlings through development of CMNs formed by AM fungi, highlighting a potential application in the restoration of degraded ecosystems in saline soils (Yu et al., 2020).

In addition to the capacity to colonize efficiently new hosts, the use of CMNs as a primary inoculum source could reduce the cost induced by AM fungi colonization during the early stage of development. Indeed, the absence of differences in e.g. P content or fresh weight between the leaves of potato plantlets newly incorporated in a CMN versus non-mycorrhizal plantlets have been measured, suggesting that the cost of establishment of AM fungi was probably smaller for the incorporated plantlets and mostly taken by the donor plant (Alaux et al., 2020; Gallou et al., 2012). Seedlings may establish more easily within an existing mycorrhizal network because they have a direct access to a large pool of soil nutrients and water through the CMN, or in some situations even directly from other plants (Van der Heijden, 2004; Voets et al., 2008).

3.2 | Distribution and retention of mineral nutrients

A key question from a management perspective is: do plants integrated into common mycorrhizal networks gain more nutrients than plants that are solely associated with an isolated community of mycorrhizal fungi? Several studies have tackled this question but the findings are inconsistent with some reporting that integration into CMNs leads to positive effects on nutrient uptake and biomass compared to non-mycorrhizal controls (Francis & Read, 1995) or isolated mycorrhizal host (Yu et al., 2020), and some others reporting negative effects (Francis & Read, 1995; Janoušková et al., 2011; Merrild et al., 2013). While in some cases experimental designs prevented a clear analysis of the role of CMNs, the elegant experiment of Merrild et al., 2013 showed clearly that CMNs led to greater size inequality and reduced P uptake by tomato seedlings connected to larger cucumber plants. Inequality was shown for N between large and small plants of big bluestem (*Andropogon gerardii* V.) emphasizing the need to consider the temporal dynamics of such responses on plant fitness, especially in grazed ecosystems (Weremijewicz

et al., 2016). For example, in the short-term grazers may favor large stature plants to their cost, while in the longer term, smaller stature plants could gain relatively greater benefit from nutrient acquisition by CMNs.

Additionally, even if CMNs do not affect net uptake of nutrients, they may affect the distribution of nutrients leading to more uniform performance amongst plant populations and communities, and may also facilitate retention of nutrients (Hamel et al., 1991) and thus potentially reduce pollution from fertilization. Arbuscular mycorrhizal fungi can regulate nutrient transfer depending on resource inequalities amongst the CMN (Welte, 2009; Whiteside et al., 2019) and inequality seems to increase trading (Whiteside et al., 2019). For example, P of different origins was translocated across the fungus in both directions, from P-poor to P-rich areas, and *vice versa*, with a greater net movement from rich to poor areas (Whiteside et al., 2019). Walder et al. (2012) found that nutrient uptake and biomass gain was greater when two plant species (*Linum usitatissimum* L. and *Sorghum bicolor* L.) were interconnected by a CMN compared to when grown as monocultures and in the absence of mycorrhizal fungi. As a result, CMNs can alter trade with hosts not only by changing the amount of phosphorus the fungi trades (Whiteside et al., 2019), but also by altering the location of P transfer within the network (Fellbaum et al., 2014; Jakobsen & Hammer, 2015; Noë & Kiers, 2018). These mechanisms may help maintain the mutualistic balance between mycorrhizal plants and fungi with both partners having control of either C or P flow (Kiers et al., 2011).

3.3 | Pest and pathogen resistance

Below-ground signaling can occur between plants infected with pests to non-infested neighbors via CMNs formed by AM fungi (Babikova, Gilbert, et al., 2013; Song et al., 2010, 2014), endophyte fungi (Vahabi et al., 2018), and ECM fungi (Song et al., 2015). CMNs formed by AM fungi can elicit defence against various biological stressors such as insect herbivores (Babikova, Gilbert, et al., 2013), herbivory-elicitors (Song et al., 2019), foliar necrotrophic fungi (Song et al., 2010), and hemibiotrophs, such as Oomycota (Alaux et al., 2020), by acting as a conduit for interplant signaling (Johnson & Gilbert, 2015). Many of these studies were undertaken on plants relevant to horticulture and agriculture such as broad bean, tomato, tobacco, and potato, reflecting the potential application of CMNs to agroecosystems. The concept of a sentinel plant, whereby susceptible plants are inspected at regular intervals for signs and symptoms of pest attack, could be developed further to consider the capacity of those plants to warn neighbors (Figure 1). However, the importance of signaling in nature remains largely unclear, especially regarding the mechanism of signal transfer (Alaux et al., 2020) and the overall fitness benefits to fungi (Babikova, Gilbert, et al., 2013). Signals have been shown to travel through CMNs of at least 20 cm in length (Babikova, Johnson, et al., 2013). The signal has been indirectly detected in terms of measurable response by the receiver plant (i.e. plant defence: genes or compounds) within 24 hr or even 6 hr after

donor plant being exposed to the stressor (Alaux et al., 2020; Song et al., 2019), with peak response on the receiver plant between 48 hr and 100 hr (Gilbert & Johnson, 2015). The duration over which signals are effective remains unknown (Gilbert & Johnson, 2017) but in recent studies appeared transitory, suggesting a priming phase (Alaux et al., 2020). Plant responses have been related to production of jasmonic acid (JA), ethylene (Eth; Alaux et al., 2020; Song et al., 2014, 2019), and salicylic acid (SA; Song et al., 2010; Zhang et al., 2019). Interestingly, the plant response (i.e. priming of plant defence) seems to activate only particular aspects of JA response (Song et al., 2019), which may limit the potential cost of induced defence as a result of CMN signal transfer. To effectively use this approach and reduce pest-related crop losses additional elements need to be investigated in field situations, notably the putative relay of the signals among plants and potential links between other CMNs (Wipf et al., 2019).

3.4 | Host dominancy and community composition

Manipulation of plant community composition in managed ecosystems may be a tractable method for enhancing the abundance and functioning of CMNs, which feedbacks positively to enhance plant performance. Such an approach is likely to have greatest relevance in mixed species (or genotype – see section below) systems, i.e. grassland, forests, and agroecosystems, where richness and relative abundance can be managed directly from planting and seeding. In grasslands, targeting subordinate and dominant plant species may be a promising approach because these two groups of plants are hypothesized to have contrasting responses to the presence of AM fungi (Urcelay & Díaz, 2003). Experimental evidence supports this view (Veresoglou et al., 2018), even when AM fungi lead to overall negative effects on plant growth. For example, dominant plants were more negatively affected by AM fungi than subordinate plants, which led to differences in dominance hierarchy (Mariotte et al., 2013). Promotion of subordinate and dominant plants may therefore have contrasting effects on the establishment of CMNs. Indeed, manipulation of species with other traits may also influence CMN formation: recent analysis of global databases of root traits suggest the propensity of plants to form mycorrhizas and 'out-source' nutrient acquisition dominates the root economic spectrum (Bergmann et al., 2020).

However, a major issue remains, in that the specific effect of plant communities on CMN abundance and function, and reciprocal effects of CMNs on plant community structure and performance, are poorly studied and unclear. Weremijewicz & Janos, 2013 found that CMNs amplified the size inequality of competing genotypes of the C4 grass *A. gerardii*, which often is the dominant species in the eastern United States prairie. More recent works showed that CMNs likely affect competition through differential responses of particular species to AM fungi. For example, the subordinate grass *Elymus canadensis* L. was largely unaffected when connected to an intact CMN compared to plants that were not, whereas CMNs had positive effects on growth of *A. gerardii* (Weremijewicz et al., 2018).

Common mycorrhizal networks may also have important effects in shaping community structure in forests comprising both ECM and AM hosts. In subtropical forests, CMNs supported by ECM plants promote seedling growth and survival, whereas CMNs from AM plants do not (Liang et al., 2020). Possible mechanisms behind these observations relate to the increased protection from pathogens conferred by ECM fungi compared to AM fungi, and also the ability of ECM plants to access a greater range of P forms, including complex organic molecules such as phytate (Liu et al., 2018).

4 | IMPACT OF MANAGEMENT PRACTICES ON ERM DENSITY AND CMN FUNCTION IN SITU

Few studies have explicitly focused on understanding how management practices may affect CMN functioning, even though fungal networks have potential to be affected (mostly) negatively by many conventional land-management practices. The evidence suggests that AM fungi have a key role in sustainable agriculture (Rillig et al., 2019; Zhang, et al., 2019) but we still lack clarity on how CMNs can further benefit these practices. In addition, other management scenarios should not be ignored, especially forestry and woodland creation and restoration (Figure 1), which is high on the political and societal agenda (Bastin et al., 2019). Furthermore high ERM density could increase C sequestration above the effects already observed in no-till management (around 115kg C /ha/year in United Kingdom; Hillier et al., 2009), and thus contribute to several possible ecosystem services provided by CMNs.

We know development of ERM and the composition of AM fungal communities are particularly sensitive to physical, chemical, and biological disturbances caused by agricultural practices (Verzeaux et al., 2017). Indeed, agronomic practices such as monoculture cropping (Daniell et al., 2001; Oehl et al., 2003), ploughing (Helgason et al., 1998; Oehl et al., 2005; Ryan & Graham, 2018), fertilization (Bhadalung et al., 2005; Chen et al., 2018; Johnson, 1993), pesticide applications (Buysens et al., 2015; Calonne et al., 2012; Channabasava et al., 2015), herbicide applications (Druille et al., 2013; Zaller et al., 2014), and long fallow periods with no host plants present (Daniell et al., 2001) can all negatively impact AM fungal population density, diversity, and efficacy (Avio et al., 2013; Oehl et al., 2004), as well as the density of ERM (Table 1). Sustainable agriculture therefore requires the use of techniques that may increase development of both ERM and CMNs, e.g. short fallow periods or no-till/direct drilling. Greater development of intra and extraradical hyphae has been shown in response to co-culture of different plant species (Derelle et al., 2012), and similar benefits may arise from agroforestry (Battie-Laclau et al., 2019) or intercropping practices.

Intercropping is already used widely and often consists of combination of plant species in order to achieve over yielding due to the complementary strategies of the partner species. For example, mixtures typically comprise combinations of cereals and legumes (Inal et al., 2007), but also plants with either C4 or C3 photosynthetic

pathways, such as maize and chili pepper (Hu et al., 2019). In addition to reducing loss of N from legumes (Hamel et al., 1991), CMNs can simultaneously improve the efficiency of the maize root system for the recovery of N excreted by co-occurring and interconnected soybeans (Hamel et al., 1991). Furthermore, AM fungal colonization increased when maize and chili pepper were intercropped and formed a CMN, with maize supplying part of the C for increasing AM fungi propagules in pepper roots. CMNs increased fruit yield via improving P distribution to chili pepper. Amongst a given CMN, the P competitive strategy differed for each plant host with notably higher ability of pepper against maize to access P (Hu et al., 2019), thus highlighting the need of careful selection of plants associated during the same cropping season.

Cover cropping has been reported to contribute to the restoration and maintenance of AM fungi (Verbruggen et al., 2010). Cover cropping during winter periods allows the maintenance of a potential AM fungal inoculum increasing colonization in the subsequent cultivated crops (Verzeaux et al., 2017). By providing sustained fungal networks, perennial plants in agroforestry could also be used to promote rapid recovery of CMNs. Indeed, herbaceous vegetation beneath trees have been shown to maintain an active AM fungal hyphal network that rapidly colonized wheat roots, even after surface tillage of the top 10 cm layer (Battie-Laclau et al., 2019). Currently work is also underway in the UK to assess the potential of hedgerows and ley strips as sources of inocula and reservoirs of AM fungal diversity in intensively managed arable systems (Holden et al., 2019). Analysis of the effects of intercropping between walnut (*Juglans nigra* L.) has demonstrated that the dense perennial root systems of the hardwood and associated herbaceous understorey vegetation allows rapid recolonization of large soil volumes and subsequent colonization of wheat roots in soils subjected to physical disruption by tillage (Battie-Laclau et al., 2019). Similar processes could operate in forests and be exploited by forest management to maximize productivity. For example, leaving occasional mature trees intact following clear-cutting can provide a source of inocula (i.e. mother plants, Figure 1) via CMNs for newly planted saplings, which has been shown to improve sapling growth (Teste & Simard, 2008).

Increasing focus has been put on the interactions between crops and weeds; AM fungi can suppress weeds if they are non-hosts (Daisog et al., 2012) that could be exploited through co-cultivated in intercropping systems. The effect of biomass removal from grazing on CMN functioning remains to be tested. The effects of grazing on AM colonization of roots is ambiguous (Barto & Rillig, 2010) partly through complex interactions with biological (e.g. plant and fungal species), edaphic and climatic variables (Faghihinia et al., 2020). Ba et al. (2012) found that grazing had a positive feedback on the relationship between AM fungi and host plants under light-to moderate-grazing, but has negative effects under heavy-grazing.

One aspect of crop management that has received limited focus is the potential to use mixtures of crop varieties rather than monocultures, either within a field or between years. Often perceived as generalists, AM fungi can develop strong genotype-specific interactions with plants (Cosme et al., 2018). Although data on the ability

of different crop varieties to produce ERM and form CMNs is lacking, Plouznikoff et al. (2019) linked quantitative trait loci (QTLs) to greater AM fungi colonization in tomato (from 15% to 92%). There is strong evidence that varieties of arable crops, such as wheat, vary considerably in their susceptibility and response to AM fungi (e.g. Hetrick et al., 1992), as well as in other ecologically important traits. Therefore, we expect ERM production to be also dependent on host genotype identity, and creating mixtures within a field or between growing seasons offers promise to enhance ecosystem services and productivity (Barot et al., 2017).

Finally, CMNs may promote transfer of larger molecules, and even microbes, that have potential to affect plant growth either positively or negatively. For example, CMNs have been shown to facilitate bacterial translocation (de Novais et al., 2020), suggesting that simultaneous associations of plants with AM fungi and beneficial bacteria is possible. This observation may pave the way for new delivery mechanisms of biofertilizers (i.e. “super spreader”, Figure 1), biostimulants and biocontrol agents (du Jardin, 2015; Velivelli et al., 2014), but may also make plant populations interconnected by CMNs susceptible to infection. Colonization of roots by AM fungi tends to increase susceptibility of plants to viruses (i.e. mycorrhiza induced susceptibility (MIS); Miozzi et al., 2019), and so research is needed to explore whether CMNs have a role in accelerating MIS. In addition, the ability of mRNA to move between parasitic plants and their hosts via roots (Kim et al., 2014) also raises questions whether CMNs can facilitate transfer of genomic information.

5 | SYNTHESIS AND FUTURE DIRECTION

Humans need to make a step-change in how land is managed if we are to tackle society's grand challenges and the sustainable development goals set out by the United Nations. Capitalizing on the functional attributes of mycorrhizal fungi offers promise (Figure 1), but we highlight that greater explicit focus on CMN ubiquity, functioning, and response to management interventions is needed to gain a much-needed ‘holistic’ view of how mycorrhizal fungi can be managed to enhance ecosystem services. A popular view of CMNs is that they offer many benefits for the functioning of ecosystems, but we highlight that the evidence supporting such views is limited, with negative effects of CMNs on plant performance being reported in some cases. A basic issue concerns the relative effect (positive or negative) of CMNs on plant performance and other ecosystem services versus the effects arising from simply forming mycorrhizas. Just how much added-value do CMNs bring? For example, the effect of CMNs in driving size inequality of plants may matter less to farmers if plants gain better protection from pests as a result of being connected to a CMN. It is vital that key knowledge gaps are filled, notably the need to characterize under field conditions the AM species involved in the formation of CMNs. Furthermore, a consistent approach to experimentation, data collection, and synthesis among mycorrhizal type would also be beneficial; consideration of P uptake remains a

focus in AM systems, but the role of P in ECM systems is relatively poorly studied.

We highlight the need for further basic and applied research on the ubiquity and function of CMNs in nature in order to inform land-management policy and guidance. Notably, we need to know under which circumstances do CMNs really have value for land-managers? And can CMNs ever be considered as separate from mycorrhizal colonization in nature, and therefore explicitly influenced by management? Answering such questions is vital not just in managed systems but also from a fundamental ecological context.

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AUTHOR CONTRIBUTIONS

P-LA, YZ, and DJ wrote the manuscript. YZ collected data used in table and made the summary figure. LG contributed manuscript editing and provided central feedback. DJ and LG secured the funding.

ORCID

Pierre-Louis Alaux  <https://orcid.org/0000-0002-2518-7911>

Yaqian Zhang  <https://orcid.org/0000-0002-7172-4503>

Lucy Gilbert  <https://orcid.org/0000-0002-9139-8450>

David Johnson  <https://orcid.org/0000-0003-2299-2525>

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